

UNGULATE MORTALITY AND SEDIMENTARY FACIES IN THE LATE TERTIARY VARSWATER FORMATION, LANGEBAANWEG, SOUTH AFRICA

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(With 7 figures and 3 tables)

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ABSTRACT

Dental crown heights are used to establish mortality profiles for the giraffids *Sivatherium hendeyi* and *Giraffa* sp., the bovids *Mesembriportax acrae* and *Simatherium demissum*, and the rhinoceros *Ceratotherium praecox* from the early Pliocene Varswater Formation. The giraffid mortality profiles exhibit classic 'catastrophic' shapes, in which progressively older age classes contain progressively fewer individuals, similar to the age structure of a live population of large mammals. This suggests that the giraffids died from a cause that does not select with respect to age. Since the giraffid remains come from an ancient river channel, the most probable cause is drowning during flood periods. Giraffid bones far outnumber those of other species in the channel fill, suggesting that the giraffids were particularly prone to drowning, probably because their feeding habits tied them to the proximity of the river even during flood intervals. The mortality profiles of the other species all exhibit 'attritional' shapes, in which prime-age adults are seriously under-represented relative to their probable live abundance. For the rhinoceros and a portion of the *M. acrae* individuals, the remains of which accumulated subaerially on the estuarine floodplain adjacent to the river channel, the implication is that death was due mainly to predation, accidents, endemic disease, and other mortality factors that disproportionately affect the very young and the old. For the remainder of the *M. acrae* individuals and for *S. demissum*, the remains of which came from the same channel fill as the giraffid bones, it seems likely that death by attritional causes was followed by secondary incorporation of bones in the river channel.

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THE LANGEBAANWEG FOSSIL SITE

The occurrence of vertebrate fossils exposed by open-cast phosphate mining at Langebaanweg (18°9'E 32°58'S) (Fig. 1) was first reported in 1958 (Singer & Hooijer 1958; Singer 1961). Research since then, supervised mainly by Q. B. Hendey of the South African Museum, has led to a vast accumulation of specimens, making Langebaanweg one of the most prolific sources, if not the

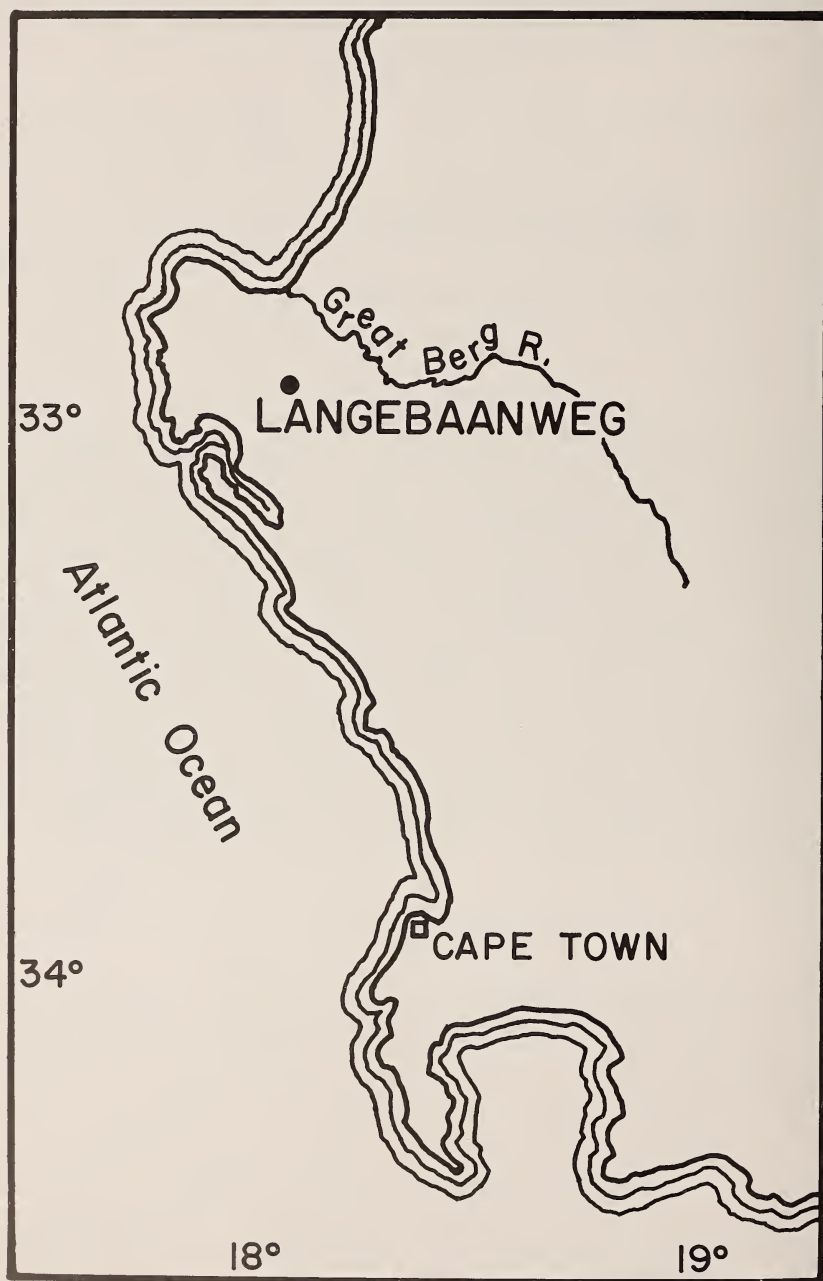


Fig. 1. The approximate location of Langebaanweg.

most prolific source, of late Tertiary vertebrate fossils anywhere in the world. Henzey (1970*a*, 1970*b*, 1972*a*, 1973, 1974, 1976*a*, 1981; Henzey & Deacon 1977) has published periodic overviews of the site, as well as descriptions and analyses of the carnivore taxa represented in the deposits (Henzey 1972*b*, 1974, 1977, 1978*a*, 1978*b*, 1980; Henzey & Repenning 1972; De Muizon & Henzey 1980). Specialist reports have also appeared on the invertebrates (Kensley 1972, 1977; Tankard 1975), penguins (Spheniscidae) (G. Simpson 1971, 1975, 1979), other birds (Rich 1980), micromammals (Pocock 1976), proboscideans (Maglio & Henzey 1970; Maglio 1973: 51 ff.), perissodactyls (Boné & Singer 1965; Hooijer 1972, 1976), peccary (Tayassuidae) (Henzey 1976*b*), giraffids (Harris 1976), and bovids (Gentry 1974, 1980).

By far the most important source of fossils at Langebaanweg has been the open-cast phosphate mine known as the New Varswater Quarry or, more informally, as 'E' Quarry, whose sedimentary sequence has been discussed by Bishop (1980), Butzer (1973), Dingle *et al.* (1979), and Henzey (various review papers cited above, especially 1981). The lowermost unit exposed in 'E' Quarry consists of phosphatic pebbles and cobbles in an unconsolidated sand matrix. Both invertebrate and vertebrate fossils are relatively abundant, while marine taxa predominate very heavily. The deposit is clearly of marine origin and was formed when the Atlantic coast, presently located 13 km to the west, intersected the area exposed by the quarry.

Nonconformably overlying the marine unit are the deposits which have provided the vast majority of terrestrial fossils from 'E' Quarry, including all those discussed here. These deposits, assigned to the Varswater Formation, comprise two principal units, referred to by Henzey as the Quartzose Sand Member (older) and Pelletal Phosphorite Member (younger).

The Quartzose Sand Member (QSM) consists primarily of fine-grained, non-phosphatic, white quartz sands reaching a thickness of up to 2 m. Lateral gradation into salt marsh and tidal mudflat sediments indicates that the sands were laid down on the estuarine floodplain of a river that probably entered the sea to the south-west of 'E' Quarry. The sands and associated facies contain both vertebrate and invertebrate fossils, but terrestrial vertebrates predominate. Abraded bones are rare, while partial, semi-articulated skeletons are common. Post-mortem fluvial disturbance of skeletons is believed to be minimal; scavengers and other biological agents were probably responsible for most bone disarticulation, displacement, and destruction.

The Pelletal Phosphorite Member (PPM) consists of up to 20 m of relatively coarse, generally well-sorted sands incorporating a variable quantity of phosphate pellets. Commercial exploitation centres on these deposits. Fossils are sparse through much of the deposit, but very substantial concentrations occur in the subunits named Beds 3aS and 3aN, which represent successively more northerly channel fills of the same river that was responsible for deposition of the Quartzose Sand Member. Vertebrate fossils predominate heavily, and terrestrial forms are best represented. In contrast to the situation in the QSM, in

the PPM abraded bones are common, and partial, semi-articulated skeletons are virtually unknown. The majority of bones are believed to have been deposited by the ancient river on bars within its channel.

There are no materials suitable for radiometric age determination at Langebaanweg, but it is possible to estimate the age of the deposits by comparing the taxa they contain to taxa found in dated contexts elsewhere (especially in east Africa) and by a consideration of the global sea-level and climatic events that are reflected in the Langebaanweg geologic sequence. On this basis, Hendey (1981) has concluded that the marine unit at the base of the sequence is probably of middle to late Miocene age, while the QSM and PPM are probably about 5 million years old, or early Pliocene as the term is presently defined.

The river, which was primarily responsible for the deposition of the QSM and PPM sediments, was almost certainly the precursor of the modern Great Berg, which now flows into the sea 20 km north of Langebaanweg from an origin in the mountains of the south-western Cape 70 km and more to the east (Fig. 1). In a broad sense, the channel and estuarine floodplain of the Great Berg provide analogues for the depositional environment of the QSM and PPM, although the QSM and PPM fossil assemblages point to a very different climatic and biotic setting than the historic one. Perhaps most striking is the presence of giraffids, which are particularly abundant in the PPM. Giraffids were totally absent in the historic fauna of the region, reflecting the historic absence of suitable browse trees. Tree growth in early Pliocene times was probably promoted by higher annual rainfall (the historic average near Langebaanweg is about 250 mm/a), perhaps combined with a different seasonal distribution of rainfall (presently confined almost entirely to the winter months). Greater rainfall may be more directly inferred from the QSM and PPM sediments, which indicate that the ancient river carried substantially more water than the historic Great Berg, at least seasonally.

Although essentially the same mammalian taxa are represented in both the QSM and the PPM, their relative abundance varies dramatically between the two units. Generally speaking, there is a tendency for several species to be subequally represented in the QSM, with no single species dominating overwhelmingly. In contrast, in the PPM, alcelaphine antelopes (*Damalacra* spp) and giraffids (*Giraffa* sp. and especially *Sivatherium hendeyi*) are superabundant v. other species. Within the PPM, alcelaphines dominate heavily in Bed 3aS and giraffids in 3aN. Since Beds 3aS and 3aN were deposited under similar circumstances—both are primarily channel fills of the proto-Great Berg—the difference in their fossil contents may reflect vegetational change, from more open vegetation in 3aS (dominated by grazing alcelaphines) to more closed (wooded) vegetation in 3aN (dominated by browsing giraffids). Vegetational change may also account for the superabundance of alcelaphines and giraffids in the PPM v. the QSM, but it seems equally possible that the alcelaphines and giraffids are so common because they were much more likely to drown than other species and thus had a far higher probability of becoming incorporated in channel sediments.

The implication would probably be that the alcelaphines and giraffids were more inclined than other species to remain near the river for feeding (?the giraffids) or to attempt crossings (?the alcelaphines) during periods of (?seasonally) high flow.

Flooding as a cause of death tends to select its victims without regard for age. Therefore, if the alcelaphines and giraffids are superabundant in the Bed 3aS and 3aN channel fills, at least in part because these species were especially prone to drowning during flood periods, analysis of their remains may be expected to produce age (= mortality) profiles in which the age structure of the original live populations is closely mirrored. In contrast, if animals represented in the QSM died primarily from predation, endemic disease, accidents, etc. on the ancient floodplain, analysis of their remains should produce age profiles in which those classes most prone to death by predation, etc.—the very young and the old—are disproportionately well represented compared to their initial live abundance. Mortality profiles reflecting death from an agency such as flooding that is non-selective with respect to age are sometimes called 'catastrophic', while profiles reflecting death from predation, accidents, endemic disease, and other causes that disproportionately affect the very young and the old are sometimes called 'attritional' (Voorhies 1969, with references).

This paper presents mortality profiles for some pertinent QSM and PPM ungulate species in order to help determine whether differences in relative taxonomic abundance between the units reflect vegetational change or the difference in depositional facies. More generally, the mortality profiles are obviously relevant for reconstructing the ancient Langebaanweg environment, as well as the behaviour of its inhabitants. Finally, the profiles may be compared to those from other sites, for example those where bones were accumulated by people, to help explain the nature of ungulate mortality there.

MATERIALS AND METHODS FOR CONSTRUCTING AGE (= MORTALITY) PROFILES

In general, teeth monitor advancing age more closely than any other element in mammals. At Langebaanweg, as in most fossil assemblages, they are also among the easiest elements to identify taxonomically, and they are also relatively abundant because of their durability. These are the reasons that teeth were chosen to construct age profiles for various QSM and PPM taxa.

The taxa to be analysed were selected partly for their absolute abundance in the QSM or the PPM and partly for their suitability to age determination by the method discussed below. The rhinoceros, *Ceratotherium praecox*, and the boselaphine antelope, *Mesembriportax acrae*, were the most suitable species in the QSM, while the giraffids, *Sivatherium hendeyi* and *Giraffa* sp., the buffalo, *Simatherium demissum*, and the boselaphine, *M. acrae*, all as represented in Bed 3aN, were the most suitable examples in the PPM.

The *Giraffa* sample almost certainly includes some teeth from the dentally very similar *Palaeotragus* cf. *germaini*, an okapi-like giraffid represented by

ossicones in Bed 3aN. However, the relative rarity of the ossicones, combined with the homogeneity of the *Giraffa* dental samples, as reflected in relatively small coefficients of variation (Table 1), suggests that 'contamination' by *Palaeotragus* is probably very limited.

A more serious possibility of taxonomic mixture exists in the Bed 3aN boselaphine sample, in which the coefficients of variation are very large (Table 1), confirming a visual impression of substantial size variability. On average, the Bed 3aN boselaphine teeth are significantly larger than their QSM counterparts (Fig. 6 and Table 1), and it is possible that the 3aN sample reflects a rapid trend

TABLE 1

Sample size (N), mean ($\bar{x}$), standard deviation (s), and coefficient of variation ($V = 100s/\bar{x}$) for measurements of basal breadth and unworn crown height on selected teeth of *Ceratotherium praecox*, *Sivatherium hendeyi*, *Giraffa* sp., *Simatherium demissum*, and *Mesembriportax acrae* in the Quartzose Sand Member and Bed 3aN of the Pelletal Phosphorite Member, 'E' Quarry, Langebaanweg. The measurements are defined in Figures 2 to 6 and presented in millimetres. G. Simpson *et al.* (1960) suggest that biologically homogeneous samples generally exhibit coefficients of variation that are less than 10. A coefficient of more than 10 may indicate that a sample includes specimens from more than one species. The data presented below suggest that species admixture may be a problem with respect to the sample attributed to *Mesembriportax acrae* in Bed 3aN.

	dP ⁴				P ⁴			
	N	$\bar{x}$	s	V	N	$\bar{x}$	s	V
<i>Ceratotherium praecox</i> (QSM)								
basal breadth	10	55,65	2,34	4,13	43	70,32	3,46	4,92
unworn crown height	—	—	—	—	1	65,1	—	—
	dP ₄				M ₃			
	N	$\bar{x}$	s	V	N	$\bar{x}$	s	V
<i>Sivatherium hendeyi</i> (3aN)								
basal breadth	324	20,45	1,52	7,43	153	33,98	1,79	5,27
unworn crown height	—	—	—	—	42	42,78	2,28	5,33
<i>Giraffa</i> sp. (3aN)								
basal breadth	51	14,93	1,26	8,44	46	34,88	1,37	5,51
unworn crown height	4	15,08	1,26	8,36	10	27,02	0,73	2,70
<i>Simatherium demissum</i> (3aN)								
basal breadth	2	12,75	1,06	8,31	15	19,05	1,30	6,82
unworn crown height	—	—	—	—	—	—	—	—
<i>Mesembriportax acrae</i> (QSM)								
basal breadth	7	9,40	0,58	6,17	17	15,18	1,09	7,18
unworn crown height	—	—	—	—	—	—	—	—
<i>Mesembriportax acrae</i> (3aN)								
basal breadth	4	10,18	0,98	9,63	21	17,05	2,77	16,25
unworn crown height	—	—	—	—	1	27,2	—	—

towards increasing size in *Mesembriportax acrae* in 3aN times, or a mixture of specimens from *M. acrae* and a larger (unidentified) boselaphine, or from *M. acrae* and a larger, dentally very similar tragelaphine. Sorting out the alternatives remains a goal of future research. For the moment, the possibility of sample mixture limits, but does not entirely rule out, interpretation of the Bed 3aN boselaphine age profile.

The two alcelaphine antelope species (*Damalacra neanica* and *D. acalla*), that are superabundant in Bed 3aS and that are perhaps the best represented species in the composite Langebaanweg assemblage, were excluded from consideration because criteria to separate their teeth have not yet been developed. A search for such criteria is planned, and if none are found, a mortality profile based on mixed samples will be presented in a future paper. Future research should also permit the presentation of profiles for several additional ungulate species represented in the QSM, the PPM, or both, and perhaps also for some well-represented carnivores.

In theory, at least three basic methods exist for estimating individual age from teeth (see Morris 1972 or Spinage 1973 for general reviews). The first involves counting the number of growth increments or 'annuli' in cementum on the roots of teeth. In many species, including close living relatives of some that are important here, annuli counts have been shown to correlate closely with age. A more obvious, but generally less accurate method of age determination is subjective evaluation of dental eruption and wear. Finally, age may be estimated by measuring a dental dimension, particularly crown height, that clearly varies with age.

Cementum annuli are often difficult to observe and count in fossils (Spiess 1979), and the preparation of teeth for examination is time-consuming and destructive. Subjective evaluation of dental eruption and wear generally results in age classes that differ greatly among themselves in the number of months or years that each covers. Additionally, the method works best with whole dentitions, while the Langebaanweg samples consist mainly of teeth that were isolated from jawbones during mining operations. These considerations leave crown height measurements as the most practical alternative for estimating the ages of individual Langebaanweg ungulates.

The mathematical relationship between advancing age and decreasing crown height has not been established for most living species and cannot be established for those from Langebaanweg, all of which are extinct. However, for hypsodont ungulates such as the Langebebaanweg species of concern here, it has been argued that the following assumptions permit useful estimates of age from crown height (Klein 1978; Klein *et al.* 1981):

- (i) that reduction in crown height is roughly constant through the life of a tooth, that is, that the relationship between decreasing crown height and advancing age is approximately linear;
- (ii) that for a deciduous tooth, the chronological age of complete crown reduction—when the crown is all but worn away—is the age when the tooth is replaced by a permanent tooth. For a permanent tooth, the chronological age of complete crown reduction is the age past which no individuals survive in the wild, sometimes known as 'potential ecological longevity'. The dental eruption/replacement schedules and potential ecological longevities of extinct species may be inferred from those of their closest living relatives of similar size and morphology. Estimates inferred for pertinent

Langebaanweg species are presented in Table 2. It is possible to show mathematically that only very large errors in these estimates will materially affect the shape of age profiles based on them (Klein *et al.* 1981);

(iii) that the amount of crown height lost per unit time on a deciduous tooth equals the initial unworn crown height divided by the time interval between age of eruption (usually birth) and age of replacement by a

TABLE 2

Ages of dental eruption and replacement and of potential ecological longevity inferred for the Langebaanweg species considered in this paper. All figures are in years.

	dP ⁴		P ⁴		Potential ecological longevity	Basis for inference
	Age of eruption	Age of replacement	Age of eruption	Age of replacement		
<i>Ceratotherium praecox</i>	0	6	6		35	Data on the dentally very similar black rhinoceros (<i>Diceros bicornis</i>) (Goddard 1970)
	dP ₄		M ₃		Age of replacement	Basis for inference
	Age of eruption	Age of replacement	Age of eruption	Age of replacement		
<i>Giraffa</i> sp.	0	4,5	3,5		28	Data on the dentally very similar modern giraffe (<i>Giraffa camelopardalis</i>) (Hall-Martin 1976)
<i>Sivatherium hendeyi</i>	0	6	4,67		37,24	Assumption that <i>S. hendeyi</i> parameters would exceed those of modern giraffe by roughly the same (1/3) proportion that <i>S. hendeyi</i> teeth exceed modern giraffe teeth in size
	dP ₄		M ₃		Potential ecological longevity	Basis for inference
	Age of eruption	Age of replacement	Age of eruption	Age of replacement		
<i>Mesembriportax acrae</i>	0	2,5	2		18	Data on extant bovids of similar size, such as Lichtenstein's hartebeest (<i>Alcelaphus lichtensteini</i>) (Mitchell 1965), black wildebeest (<i>Connochaetes gnou</i>) (Von Richter 1971, 1974), and greater kudu (<i>Tragelaphus strepsiceros</i>) (C. Simpson 1966)
<i>Simatherium demissum</i>	0	3,5	2,5		20	Assumption that <i>S. demissum</i> parameters would be smaller than those of the Cape buffalo (<i>Syncerus caffer</i>) (Grimsdell 1973; Sinclair 1977) by roughly the same (1/4) proportion that <i>S. demissum</i> teeth are smaller than Cape buffalo ones

permanent tooth. The amount of crown height lost per unit time on a permanent tooth equals the initial unworn crown height divided by the time interval between age of eruption and age at 'potential ecological longevity'. Initial crown height may usually be estimated from unworn or lightly worn teeth present in any sample large enough to calculate an age profile. The initial crown heights used in this study are presented in Table 3. It may be shown mathematically that only a very large error in estimated initial crown height will materially affect the shape of an age profile (Klein *et al.* 1981).

The key assumption here is that the rate of crown height reduction is constant. In the present context, it is pertinent that a more or less constant rate had been shown to characterize teeth of the Cape buffalo (*Syncerus caffer*)

TABLE 3

Initial unworn crown heights (in millimetres) used to calculate age profiles for Langebaanweg ungulate species considered in this paper. The initial unworn height of dP_4 in *Giraffa* sp. and of M_3 in both *Giraffa* sp. and *Sivatherium hendeyi* was taken as the mean height plus one standard deviation from the mean height of unworn specimens in the Langebaanweg samples. In the absence of any completely unworn specimens, the initial height of dP_4 in *S. hendeyi* was taken as the mean height plus one standard deviation from the mean height of thirteen very lightly worn specimens. *Giraffa* and *S. hendeyi* dP_4 's and M_3 's whose heights exceeded the calculated 'initial heights' were automatically assigned to the youngest age class possible.

The initial height of dP_4 in *Ceratotherium praecox* was estimated by adding 0,5 mm to the height of the highest tooth present, which was very lightly worn. The initial height of the *C. praecox* P^4 was taken as the height of the single unworn specimen present. In the absence of any unworn specimens, the initial height of dP_4 in *Mesembriportax acrae* was taken as 1 mm higher than the highest, lightly worn dP_4 in the Quartzose Sand Member sample. The initial height of the *M. acrae* M_3 was taken as 0,5 mm higher than the highest (very) lightly worn M_3 in the Bed 3aN sample. The initial height of the *Simatherium demissum* M_3 was estimated by adding 1,5 mm to the height of the highest-crowned M_3 present, which was lightly worn. There were no unworn or lightly worn *S. demissum* dP_4 's in the sample, so the initial crown height of this tooth was estimated by multiplying the ratio between *S. demissum* M_3 initial crown height and Cape buffalo M_3 initial height (36/53) by the initial height of the Cape buffalo dP_4 (24,0 mm), as determined in the author's previous work.

Given the variety of methods used to obtain initial crown heights, it is obvious that the values presented below are arbitrary to some extent, but it may be shown mathematically that only very large departures from these values would materially affect the shapes of the age profiles calculated from them.

	Initial (unworn) crown height (mm)	
	dP_4	P^4
<i>Ceratotherium praecox</i>	45,0	65,1
	dP_4	M_3
<i>Giraffa</i> sp.	16,3	27,8
<i>Sivatherium hendeyi</i>	23,4	45,1
<i>Mesembriportax acrae</i>	10,0	33,0
<i>Simatherium demissum</i>	16,3	36,0

(Grimsdell 1973) and of the giraffe (*Giraffa camelopardalis*) (Hall-Martin 1976), which are close living relatives of the Langebaanweg buffalo (*Simatherium demissum*) and giraffids (*Sivatherium hendeyi* and *Giraffa* sp.) respectively. A roughly constant rate has also been demonstrated in the Rocky Mountain elk (*Cervus canadensis*) (Klein *et al.* 1981), whose teeth are notably similar in size and morphology to those of Langebaanweg *Mesembriportax acrae*.

The elk study was undertaken specifically to check the reliability of the assumptions listed above. It was found that crown height was not a particularly accurate predictor of individual elk age, but the *distribution* of elk ages predicted from crown heights closely approximated the *distribution* of known ages, when both predicted and known ages were *grouped* into relatively broad, but analytically useful age classes. The age class used was based on 10 per cent of potential ecological longevity (approximately 16 years in elk, leading to a class interval of 1,6 years). 10 per cent of potential ecological longevity has also been used for grouping predicted ages within each species here, where it has the particular advantage of allowing direct comparison of age profiles among species that probably had very different potential longevity.

While the elk study strongly supported the use of crown heights to construct age profiles, it did suggest some modifications in the assumptions listed above. In particular, on average, elk shed their deciduous teeth before the crowns are completely worn away, and a better estimate of the (hypothetical) age of complete reduction in elk would be 'age of shedding plus 25 per cent'. On reflection, it seems likely that most ungulates shed their deciduous teeth before the crowns are completely reduced and 'age of shedding plus 25 per cent' has been used for each species in this study. Its principal effect is to place more individuals in the second 10 per cent of lifespan and fewer in the first. The elk study further suggested that permanent teeth which erupt later (e.g. M_2 or M_3) fit the assumptions of constant crown height reduction and of reduction to '0' at or very near 'potential ecological longevity' better than permanent teeth which erupt earlier (e.g. M_1). This result has been taken into account here as well.

In order to construct a profile that will include individuals of all possible ages within a species, crown heights must be measured on a category of deciduous teeth and on a category of permanent teeth. For Langebaanweg *Sivatherium hendeyi*, *Giraffa* sp., *Simatherium demissum*, and *Mesembriportax acrae*, dP_4 and M_3 were selected, mainly for the ease with which they may be recognized when isolated. In each species M_3 erupted before dP_4 was shed, so that the age profile produced from dP_4 crown heights overlaps with the one produced from the M_3 heights. In each case the overlap occurs in the second 10 per cent of lifespan, and the number of individuals assigned to that interval in the final (composite) age profile was based on either dP_4 or M_3 , whichever suggested the larger number.

In the rhinoceros, *Ceratotherium praecox*, dP_4 was shed before M_3 erupted. Use of these two teeth would thus automatically exclude some individuals, and it is obviously desirable to select another pair. Two further considerations affected the selection. First, it is difficult, if not impossible, consistently to distinguish M_1 from M_2 or M^1 from M^2 when these teeth are isolated, as most of the rhinoceros specimens were. Second, the structure of rhinoceros mandibular teeth suggests that their rate of wear may be exceptionally rapid just after eruption, seriously violating one of the assumptions behind the use of crown heights to predict age. The maxillary teeth appear structurally better suited to the assumptions. These considerations led to the selection of dP^4 and P^4 for construction of the rhinoceros age profile to be presented here, although, in fact, the one derived from dP_4 and P_4 is basically similar in shape and implications.

The dental dimension taken as crown height is essentially the same for all species and is illustrated in Figures 2 to 6. It is the minimum distance between the occlusal surface of a tooth and the base of the enamel, measured on the buccal face for mandibular teeth and on the lingual face for maxillary ones. On multilobed (or multilophed) teeth such as those of the species involved here, the measurement may be made on any lobe or loph. Measurements made on the anteriormost lobe (or loph) have been used to calculate the age profiles presented below, except in the case of *Sivatherium hendeyi*, where measure-

ments made on the second (or middle) lobe of M_3 were used. The reason is that many *S. hendeyi* M_3 's are broken, and the second lobe is easily identifiable as belonging to an M_3 , whereas the first is not. All measurements were made with Helios dial-reading calipers to the nearest tenth of a millimetre.

THE MORTALITY PROFILES AND THEIR IMPLICATIONS

Figures 2 to 6 present the age (mortality) profiles for each of the Langebaanweg species of concern here, as well as the crown height frequency distributions on which the profiles are based. The figures also show the frequency distributions of basal breadths for the same teeth whose crown heights were measured.

If each dental sample is truly homogeneous, basal breadths would probably be normally distributed, since normality is an almost universal characteristic of linear measurements on biological specimens. A significant departure from normality may indicate that dental size is sexually dimorphic or that a sample actually includes specimens from more than one species. (In either case, if enough specimens were included, the frequency distributions would be multimodal.) Applications of various tests suggested by Simpson *et al.* (1960) and Sokal & Rohlf (1969) to the Langebaanweg basal breadth distributions revealed only one significant departure from normality. This was for Bed 3aN *Mesembriportax acrae*, supporting the suggestion (above) that the sample may be taxonomically mixed.

Assuming that the relatively large samples available for *Sivatherium hendeyi*, *Giraffa* sp., and *Ceratotherium praecox* presumably reflect the populations from which they were drawn, the normal shape of the basal breadth distributions supports taxonomic homogeneity in each case and suggests that the dentitions of the species were not sexually dimorphic in size. (The alternative—that the teeth in each instance were drawn almost entirely from one sex—seems highly improbable). Perhaps even more important in the present context is that the heights of unworn crowns also appear to be distributed normally in those species (*Giraffa* sp. and especially *Sivatherium hendeyi*) where the samples of unworn crowns are reasonably large (Table 1). Generally speaking, marked sexual dimorphism in size is probably quite rare in ungulate dentitions (see, for example, the measurements on teeth of known sex in Klein 1974, 1975; Klein *et al.* 1981), which justifies ignoring sex in calculating age profiles from ungulate crown heights.

Examination of the mortality profiles presented separately in Figures 2 to 6 and recast as a group in Figure 7, shows that there are two basic types. In type one, characterizing *Sivatherium hendeyi* and *Giraffa* sp., individuals in the first 10 per cent of lifespan dominate heavily and successive lifespan segments include progressively fewer individuals, with very few beyond 40 per cent of potential lifespan. Type one is a classic 'catastrophic' mortality profile. In type two, characterizing *Ceratotherium praecox*, *Simatherium demissum*, and *Mesem-*

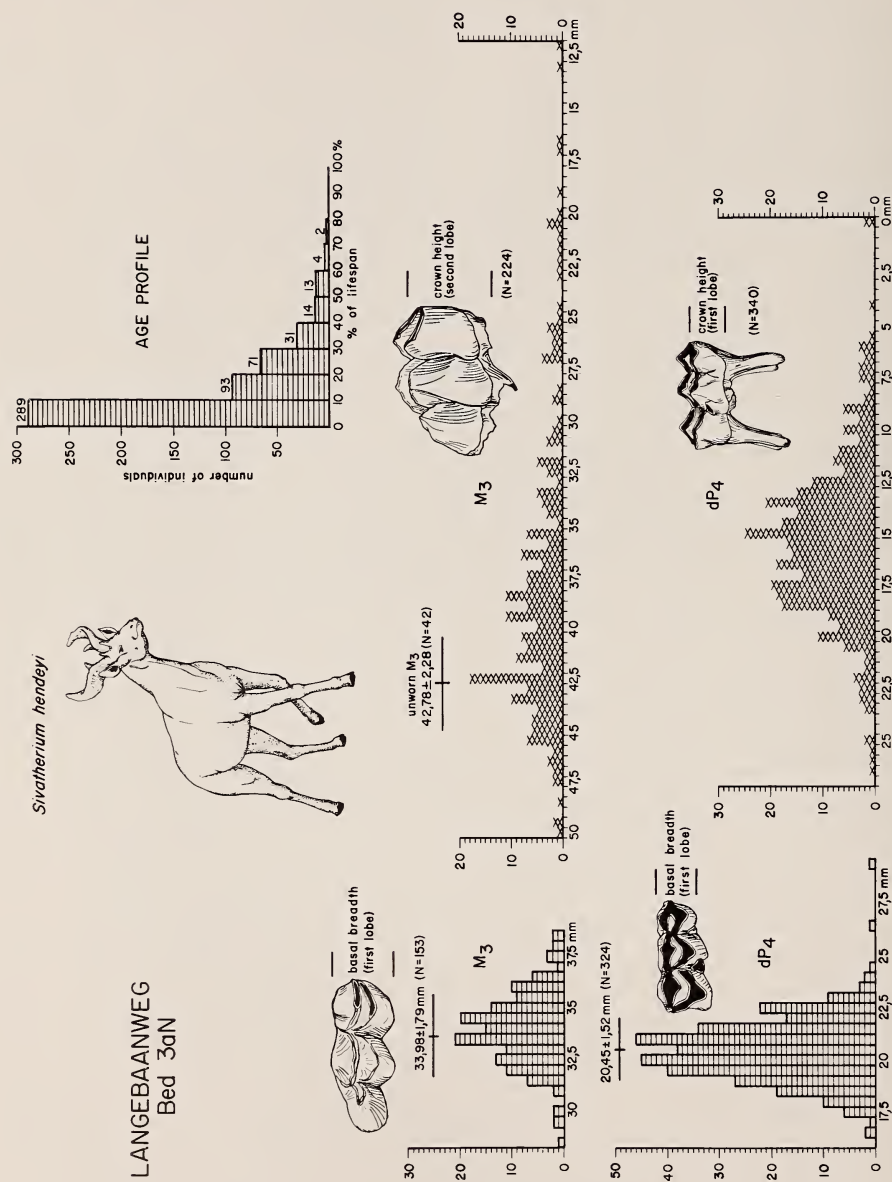


Fig. 2. The distribution of dP₄ and M₃ basal breadths and crown heights in the *Sivatherium hendeyi* sample from Bed 3aN of the Pelletal Phosphorite Member, Varswater Formation, Langebaanweg. The original measurements have been grouped into 0,5 mm classes. Means and standard deviations are presented for basal breadths and for the crown heights of unworn M₃'s. The age profile in the upper right-hand corner was calculated from the crown height distributions, as explained in the text.

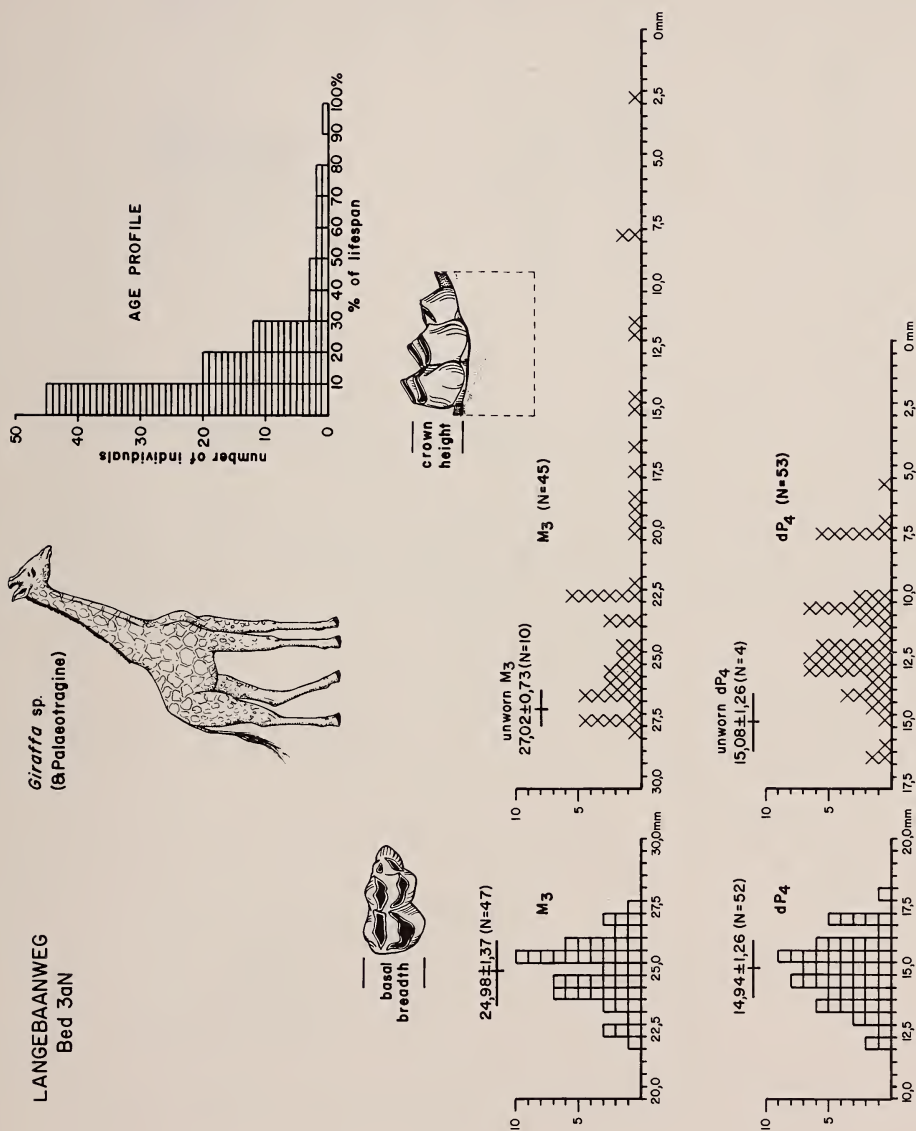


Fig. 3. The distribution of dP_4 and M_3 basal breadths and crown heights in the *Giraffa* sp. (and *Palaeotragine*) sample from Bed 3aN of the Pelletal Phosphorite Member, Varswater Formation, Langebaanweg. The original measurements have been grouped into 0.5 mm classes. Means and standard deviations are presented for basal breadths and for the crown heights of unworn teeth. The age profile in the upper right-hand corner was calculated from the crown height distributions, as explained in the text.

LANGEBAAWEG QSM

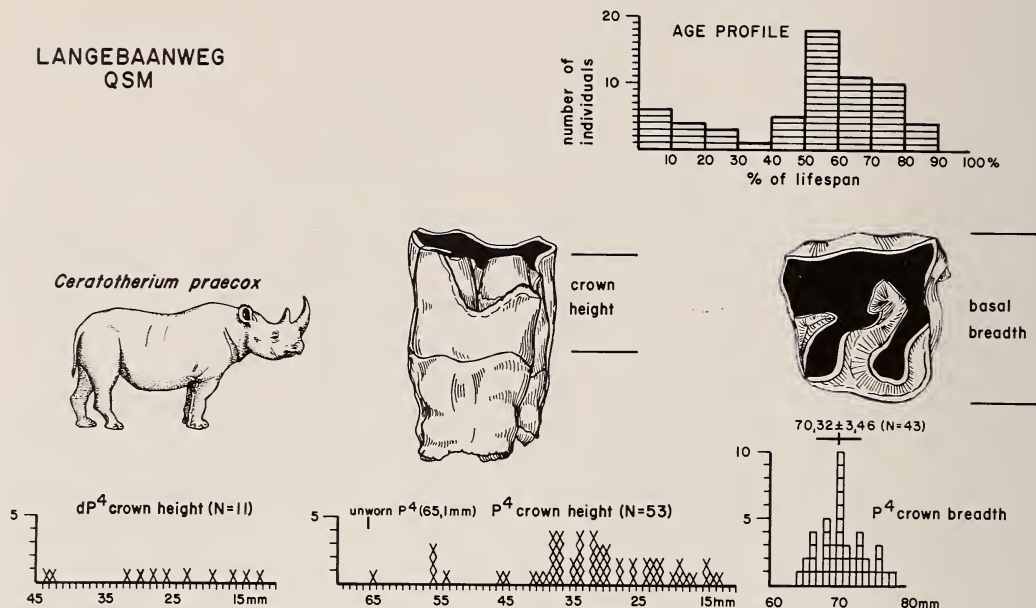


Fig. 4. The distribution of dP^4 and P^4 crown heights and of P^4 crown breadths in the *Ceratotherium praecox* sample from the Quartzose Sand Member, Varswater Formation, Langebaanweg. The original measurements have been grouped into 1 mm classes. The mean and standard deviation are presented for P^4 crown breadth. The age profile in the upper right-hand corner was calculated from the crown height distributions, as explained in the text.

LANGEBAAWEG

Simatherium demissum (3aN)

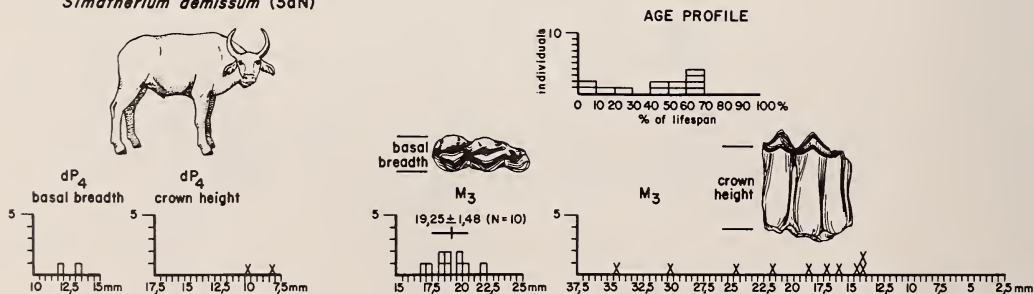


Fig. 5. The distribution of dP_4 and M_3 basal breadths and crown heights in the *Simatherium demissum* sample from Bed 3aN of the Pelletal Phosphorite Member, Langebaanweg. The original measurements have been grouped into 0,5 mm classes. The mean and standard deviation of M_3 breadth are presented. The age profile in the upper right-hand corner was calculated from the crown height distributions, as explained in the text.

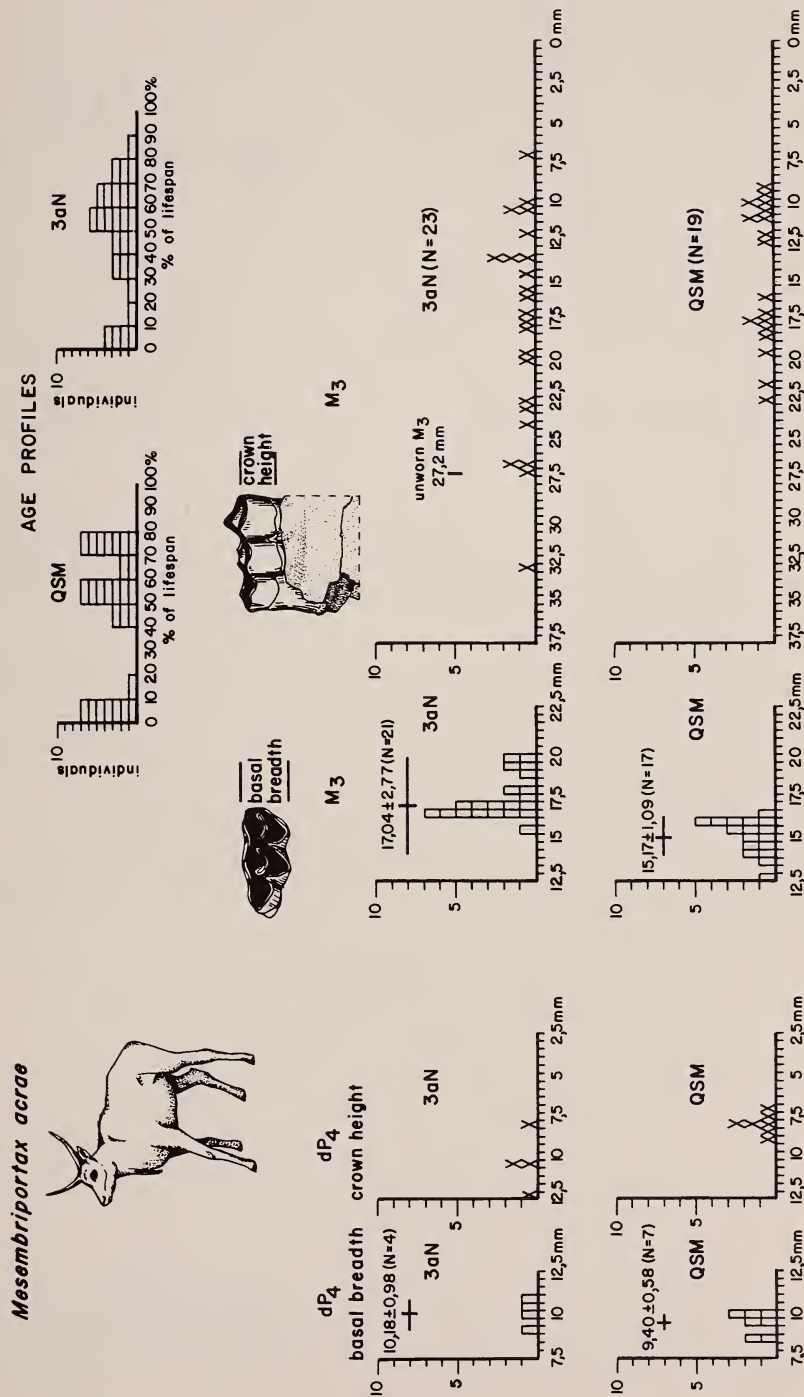


Fig. 6. The distribution of dP₄ and M₃ basal breadths and crown heights in the *Mesembriportax acrae* samples from the Quartzose Sand Member and from Bed 3aN of the Pelletal Phosphorite Member, Varswater Formation, Langebaanweg. The original measurements have been grouped into 0,5 mm classes. Means and standard deviations are presented for basal breadths. The age profiles in the upper right-hand corner were calculated from the crown height distributions, as explained in the text.

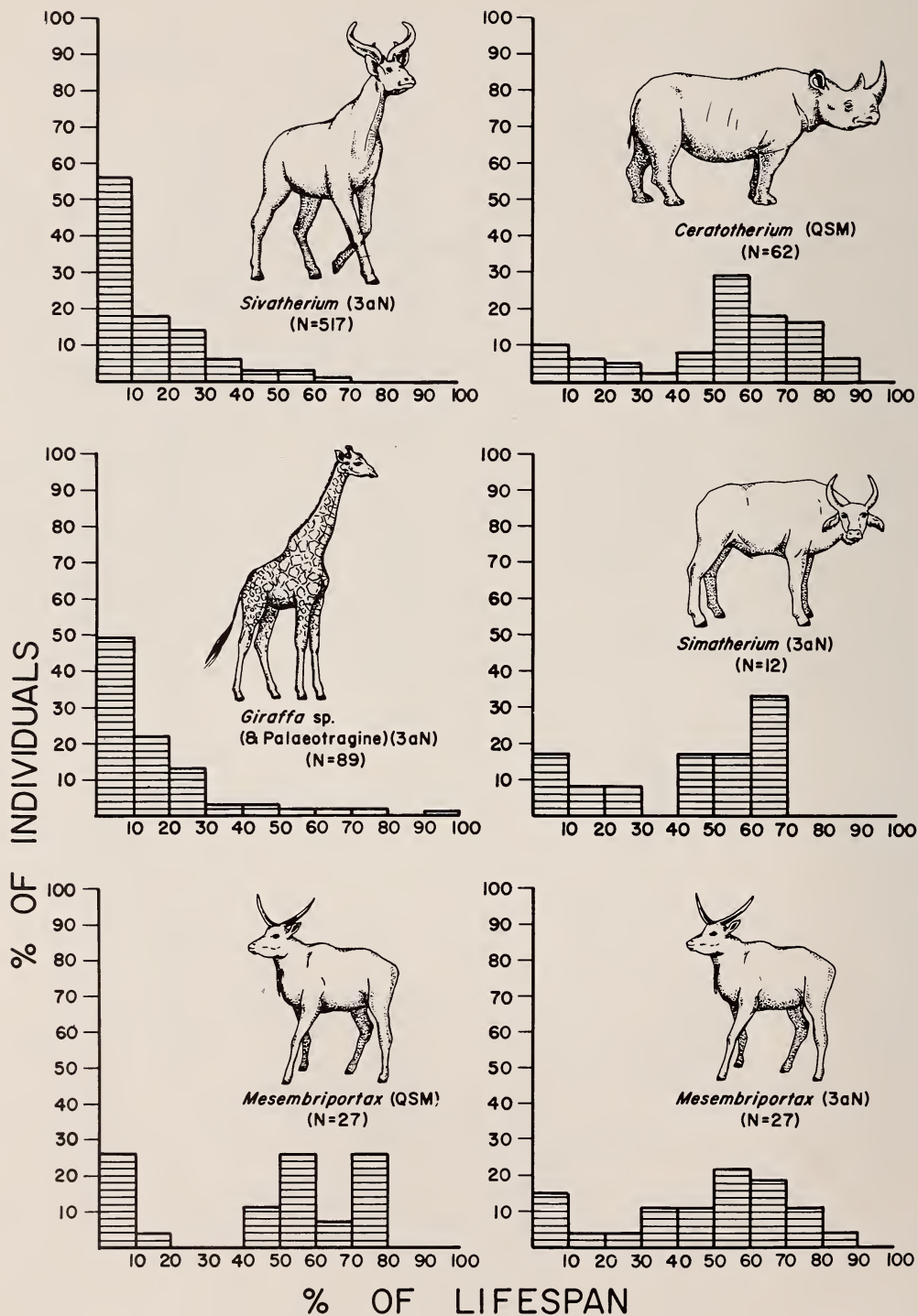


Figure 7.

briportax acrae, individuals beyond 40 per cent of lifespan predominate heavily and ones in lifespan segments between 10 and 40 per cent are particularly infrequent. Type two would be a classic 'attritional' mortality profile, except for the relative rarity of individuals in the first 10 per cent of lifespan. Application of the Kolmogorov–Smirnov test (results in the caption of Fig. 7) supports the assertion that the *Sivatherium* and *Giraffa* profiles resemble each other and differ from those of the other species, which are, however, similar to each other.

The catastrophic shape of the *Sivatherium* and *Giraffa* mortality profiles clearly suggests that the individuals present in the Bed 3aN channel fill were victims of drowning, and thus that their superabundance versus other species in the deposit may reflect a greater tendency to remain near the river during flood periods. The most likely explanation for this behaviour is that the trees on which the giraffids browsed were largely restricted to the immediate vicinity of the river. Other species, such as the rhinoceros and the boselaphine, which probably browsed on understorey plants, and the buffalo and alcelaphines, which were probably grazers, were probably attracted away from the river during flood intervals by the vegetation flush and more widely available surface-water accompanying rains.

After the giraffids, the alcelaphines are the most common species in Bed 3aN, and it is possible that, their food preferences aside, they were more prone than other species to attempt to cross the river in flood periods. Together with a reduction in the density of woodland along the river, this could account for the superabundance of alcelaphines v. other species in Bed 3aS. Although the alcelaphine crown heights have yet to be measured, subjective examination suggests that they will provide 'catastrophic' age profiles at least broadly similar to the giraffid ones.

Assuming that the giraffids are the most common species in the Bed 3aN channel fill because they were more likely than other species to be caught in floods, it would obviously be interesting to know whether flooding was seasonal

Fig. 7. Age profiles of *Sivatherium hendeyi*, *Giraffa* sp. (and Palaeotragine), *Ceratotherium praecox*, *Simatherium demissum*, and *Mesembriportax acrae* in the Quartzose Sand Member and in Bed 3aN of the Pelletal Phosphorite Member, Varswater Formation, Langebaanweg. The Kolmogorov–Smirnov results below indicate that the profiles of *S. hendeyi* and *Giraffa* sp. are statistically indistinguishable from one another, but differ significantly from the profiles of other species, which are in turn statistically indistinguishable from one another. A Kolmogorov–Smirnov value of 1,36 implies a difference significant at the 0,05 level; a value of 1,63 implies a difference significant at the 0,01 level. Values reflecting a difference significant at the 0,05 level or below are underlined.

	<i>Siva- therium hendeyi</i> (3aN)	<i>Cerato- therium praecox</i> (QSM)	<i>Giraffa</i> sp. (and Palaeo- tragine) (3aN)	<i>Mesembri- portax acrae</i> (QSM)	<i>Sima- therium demissum</i> (3aN)	<i>Sima- therium demissum</i> (3aN)
<i>Sivatherium hendeyi</i> (3aN)	—					
<i>Ceratotherium praecox</i> (QSM)	<u>4,99</u>	—				
<i>Giraffa</i> sp. (and Palaeotragine) (3aN)	<u>0,70</u>	<u>3,87</u>	—			
<i>Mesembriportax acrae</i> (QSM)	<u>3,24</u>	<u>0,69</u>	<u>2,59</u>	—		
(3aN)	<u>3,29</u>	0,61	<u>2,78</u>	0,44	—	
<i>Simatherium demissum</i> (3aN)	<u>2,09</u>	0,59	<u>1,76</u>	0,75	0,40	—

or not. If the giraffids were seasonally restricted breeders, as most modern African ungulates are (Mentis 1972), and if flooding were seasonal, crown height distributions such as those in Figures 2 and 3 could be expected to exhibit patterned multimodality (Kurtén 1953). Successive modes representing cohorts of individuals with average birth dates a year apart would be separated by equidistant gaps representing the average amount of crown height lost by each cohort between flood seasons.

Clearly, neither the *Sivatherium* nor the *Giraffa* crown height distributions in Figures 2 and 3 exhibit the kind of multimodality from which seasonality may be reasonably inferred. In the case of the *Giraffa* distributions, the reason may be relatively small sample size. In the case of the *Sivatherium* distributions, based on much larger samples, the reason may be that the species bred more or less throughout the year or that flooding (drowning) was not seasonal. In modern *Giraffa camelopardalis*, the closest living relative of *Sivatherium*, breeding peaks tend to be subtle or absent (Mentis 1972; Foster & Dagg 1972). However, it is also important to point out that *Sivatherium hendeyi* was relatively low-crowned, particularly relative to (inferred) potential individual lifespan. This means that even if breeding were seasonal, the average amount of crown height lost by an age cohort each year was relatively small and there was probably substantial overlap in crown heights between individuals of adjacent cohorts. The detection of patterned multimodality reflecting seasonal births and deaths may therefore require truly enormous samples. It is pertinent here that the author failed to find multimodality in a large sample of similarly low-crowned elk, in which seasonally restricted births and deaths were historically documented (Klein *et al.* 1981). Overall then, the giraffids are probably less than ideal species for testing the hypothesis of seasonal bone accumulation at Langebaanweg. Far more appropriate would be the alcelaphines, because they are far more hypsodont relative to (inferred) potential lifespan and because their close living relatives often exhibit well-defined birth peaks. Additionally, alcelaphine teeth are superabundant in the Bed 3aS channel fill. The possibility of using them to detect seasonal mortality is added reason for measuring their crown heights in the near future.

The mortality profiles of *Ceratotherium praecox* and *Mesembriportax acrae* in the QSM only partly support the *a priori* suggestion that QSM species would exhibit attritional patterns. This is because individuals in the first 10 per cent of lifespan are seriously underrepresented relative to their probable level of mortality from attritional factors. The situation is similar to that noted by Sinclair (1977) for Cape buffalo on the Serengeti Plain and by Goddard (1970) for black rhinoceros in Tsavo National Park. In both instances, large samples of skulls observed in the field included remarkably few individuals in the first 10 per cent of lifespan, though such individuals were known to be characterized by relatively high mortality, as in free-ranging large mammal populations generally. In both instances, the rarity of young skulls is attributed to their greater tendency to disintegrate from weathering or to be broken up by carnivores.

Assuming that the relative lack of very young individuals in the QSM profiles at least partly reflects carnivore destruction or removal of bones before burial, it becomes especially interesting that very young individuals are extremely well represented in 'attritional' profiles constructed from the crown heights of large ungulates in late Pleistocene archeological and carnivore (probable *Hyaena brunnea*) bone accumulations in southern Africa (Klein 1978 and unpublished). With regard to the archeological sites, the implication would be either that the occupants were expert at locating the carcasses of very young animals before carnivores destroyed them or removed parts to dens, or that the occupants themselves were active predators on very young animals. The latter alternative seems more plausible, given the likely desire of hominids to avoid conflict with other potential scavengers whose special senses would probably bring them to a carcass first. These considerations lead to the further suggestion that early Pleistocene hominids, hypothetically relying more heavily on scavenging, would probably produce a bone accumulation in which 'attritional' profiles were relatively deficient in very young individuals, similar to those from Langebaanweg, rather than those from later Pleistocene archeological sites.

The age profiles of Bed 3aN *Simatherium demissum* and *Mesmbriportax acrae* require comment not because they are relatively deficient in very young individuals, but because they are clearly not 'catastrophic' in a deposit where it has already been shown that catastrophic death took place. In the case of Bed 3aN *M. acrae*, it is possible that the profile has been distorted from catastrophic shape by taxonomic admixture in the sample (see above), though it is difficult to see how admixture could have this effect. Overall, since both the *S. demissum* and *M. acrae* profiles in Bed 3aN closely resemble those of the QSM species, it seems most likely that they are based on dentitions which were either reworked from the QSM deposits or which were washed off the floodplain adjacent to the 3aN channel. One obvious test of this hypothesis would be to examine bones of Bed 3aN *S. demissum* and *M. acrae* to see if they exhibit patterns of weathering or carnivore-gnawing different from those of the 3aN giraffids and perhaps similar to those of the QSM species. This will be an aspect of future research.

SUMMARY AND CONCLUSIONS

The mortality profiles constructed from dental crown heights of five Langebaanweg ungulate species belong to two clearly distinct types. Type one, in which individuals in the first 10 per cent of potential lifespan predominate and in which there are progressively fewer individuals in each succeeding lifespan segment, characterizes the giraffids, *Sivatherium hendeyi* and *Giraffa* sp., found in the channel fill deposits of Bed 3aN. The shape of the profile suggests that the giraffids died catastrophically, probably by drowning during periods of high river flow. This suggests in turn that the giraffids are superabundant v. other species in the channel fill because they were more inclined to remain near the river during flood periods. The most plausible explanation of this behaviour is that the trees on which they browsed were largely confined to the river margins.

Other species with different feeding-habits were probably attracted away from the river during flood intervals by a rain-induced vegetation flush and increase in surface water.

In the second type of mortality profile, characterizing the rhinoceros *Ceratotherium praecox* and the boselaphine antelope *Mesembriportax acrae* in the floodplain sediments of the Quartzose Sand Member, and the buffalo *Simatherium demissum* and the boselaphine *M. acrae* in Bed 3aN, individuals beyond 40 per cent potential lifespan predominate and there are relatively few individuals in lifespan segments between 10 and 40 per cent. The shape of the profiles suggests death by natural attrition (from predation, endemic disease, etc.), though individuals in the first 10 per cent of lifespan are under-represented v. their probable level of natural mortality. This is probably because their bones were particularly susceptible to weathering or to destruction or removal by carnivores before burial. The fact that the Bed 3aN profiles of *S. demissum* and *M. acrae* are very similar to those of QSM *acrae* suggests that the bones of *S. demissum* and *M. acrae* in the 3aN channel fill were either reworked from older (QSM) deposits or swept off the floodplain adjacent to the 3aN channel.

Assuming that the under-representation of very young individuals in the Langebaanweg 'attritional' profiles at least in part reflects differential carnivore destruction or removal of their bones v. those of older animals, it is potentially meaningful that very young individuals are very well represented in 'attritional' age profiles of large ungulates in late Pleistocene archeological sites in southern Africa. Since the late Pleistocene people were probably much less successful at locating fresh carcasses than other predators and/or scavengers, the implication is that they actively preyed on the young animals. If, as logic suggests, earlier Pleistocene hominids were more dependent on scavenging (and less successful at hunting), it follows that attritional profiles of ungulates in their sites would resemble the Langebaanweg ones in the under-representation of very young individuals.

The Langebaanweg assemblage includes several other species which are sufficiently well represented to permit construction of mortality profiles. Most promising in terms of their abundance are the alcelaphines, *Damalacra neanica* and *D. acalla*, which probably also have the greatest potential for revealing whether flooding by the ancient Langebaanweg River was seasonal or not. In future research with the Langebaanweg assemblage, the author will focus on measurement and analysis of the alcelaphine material, as well as on age (and possible sex) determination in other well-represented species.

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